

CHROMOSOME NUMBERS OF SOME NORTH AMERICAN SCROPHULARIACEAE, MOSTLY CALIFORNIAN

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ABSTRACT

Chromosome counts are reported for 55 collections of 38 species representing eight genera in Scrophulariaceae, mostly from California. Chromosome numbers of 17 species are reported here for the first time, including *Collinsia linearis*, *Lamarouxia dasyantha*, *Mimulus arenarius*, *M. bicolor*, *M. bolanderi*, *M. breweri*, *M. filicaulis*, *M. layneae*, *M. latidens*, *M. pictus*, *M. pilosellus*, *M. pygmaeus*, *M. torreyi*, *M. tricolor*, *Pedicularis attolens*, *P. semibarbata*, and *Penstemon purpusii*. The species of *Lamarouxia* do not appear to be cytologically uniform as haploid numbers of $n=7$, 14, 15, and 16 have been recorded. The counts of $n=9$, 18 for *Mimulus primuloides* differ from a previous report of $n=17$. Consistency of chromosome number appears to be characteristic of certain genera of Scrophulariaceae whereas variation due to polyploidy and aneuploidy occurs in others, especially the large, polymorphic genera *Mimulus* and *Veronica*.

The Scrophulariaceae (Figwort or Foxglove Family), a large family of about 4000 species of mostly herbs or small shrubs, is distributed worldwide, but especially in the northern temperate zone. Some herbaceous genera (tribe Pedicularae) are root hemi-parasites, obtaining water and mineral nutrition from the host plants. A few genera, such as *Lathraea*, *Harveya*, and *Hyobanche*, are without or almost devoid of chlorophyll, and represent the most truly parasitic members in the family; these have been transferred back and forth between Scrophulariaceae and Orobanchaceae (Boeshore 1920; Kuijt 1969). These holoparasitic genera have usually been retained in Scrophulariaceae because they possess a bilocular ovary and axile placentation, rather than a unilocular ovary and parietal placentation as found in Orobanchaceae. The family is usually characterized by possession of an herbaceous habit, a more or less zygomorphic corolla, 2–4 stamens (plus occasionally a staminodium), a superior ovary with 2 united carpels and axile placentae, and seeds containing endosperm. Variation of these features, however, leads to uncertainty regarding proper delimitation of the family. Knowledge of Scrophulariaceae and its internal and external relationships is still far from satisfactory, as clearly pointed out by Thieret (1967). He

remarked that, "New and detailed research on the family, using whatever tools are available, and a re-evaluation of past research are necessary before a logical taxonomic treatment of the family can be realized."

On the basis of corolla aestivation and leaf arrangement, the family has traditionally been divided into three subfamilies since the treatment proposed by Bentham (1846, 1876), and later modified by Wettstein (1891). These three subfamilies are: 1) Verbascoideae (=Pseudosolanoideae, two tribes and about 10 genera, characterized by the upper corolla lip covering the lateral lobes in bud, alternate leaves, and a fifth stamen often present); 2) Scrophularioideae (=Antirrhinoideae, seven tribes and more than 100 genera, characterized by the upper corolla lobes covering the lateral lobes in bud, at least the lower leaves opposite, and a fifth stamen becoming staminodial or absent); 3) Rhinanthoideae (three tribes and more than 100 genera, characterized by the upper corolla lobes being covered by one or both lateral lobes in bud, either alternate or opposite leaves, and a fifth stamen absent).

In a broad review of chromosome numbers in angiosperms, Raven (1975) pointed out that, "Scrophulariaceae are extremely diverse cytologically and the overall pattern is difficult to determine. Many of the tribes appear to be characterized by descending aneuploidy, but it is not certain whether any of the original diploids persist in most of them or not." Published reports of chromosome numbers of western North American Scrophulariaceae, particularly from California, are numerous, consisting either of scattered data on individual species or in taxonomic revisions and monographs of certain genera. Especially significant contributions to the cytotaxonomy of western American Scrophulariaceae have been those of Keck (1945) on *Penstemon*, McMinn (1951) on *Diplacus* (= *Mimulus*), Garber (1956) on *Collinsia*, Vickery (1978, summarized the reported counts) on *Mimulus*, Heckard (1968) on *Castilleja*, Chuang and Heckard (1982) on *Orthocarpus*, Chuang and Heckard (1973, 1975, 1986) on *Cordylanthus*, and Thompson (1988) on *Antirrhinum*.

Our study of *Cordylanthus* showed diversity in chromosome number that proved useful in infrageneric classification (Chuang and Heckard 1986). Each chromosome number, except $n=14$, coincides well with a particular group of related species (subgenus *Dicranostegia* $n=16$; subgenus *Hemistegia* $n=14, 15, 21$; subgenus *Cordylanthus*, $n=14$ for section *Cordylanthus*, $n=13$ for section *Anisocheila*, and $n=12$ for section *Ramosi*). The observed differences in base chromosome numbers ($n=11, 12$, and 14) in *Orthocarpus* (Chuang and Heckard 1982), and correlation of cytological information with different corolla morphology, stigma shape, ovule type, and seed coat morphology strongly support our contention that the genus as previously defined (*sensu* Keck 1927) is a heterogeneous and prob-

ably polyphyletic group (Chuang and Heckard 1991). We realigned the members of *Orthocarpus* into three genera: 1) *Orthocarpus*, restricted to the type section and subgenus with $n=14$; 2) *Castilleja* section *Oncorhynchus*, including Keck's (1927) sections *Castillejooides* and *Cordylanthoides*, with $n=12$; and 3) *Triphysaria*, an elevation of subgenus *Triphysaria* to generic status, with $n=11$ (Chuang and Heckard 1991). Our continuing survey of chromosome number in *Castilleja* (Heckard 1968; Heckard and Chuang 1977, and unpublished data) shows that over one-half of 100 species examined are either polyploid or are diploid plus one or more polyploid levels. For example one species complex, *Castilleja affinis-litoralis*, has diploids plus 5 levels of polyploidy from $4x$ to $12x$. The widespread *C. miniata* of western United States and Canada has diploids and four additional levels of ploidy from $4x$ to $10x$. Our preliminary study of the relationship of polyploidy to morphological variation indicates that hybridization and the widespread occurrence of polyploidy have resulted in formation of extensive pillar polyploid complexes, often with intergradation on a large scale.

A steady increase in knowledge of chromosome numbers may play an important role in placing taxa of uncertain affinities, in suggesting realignments, and corroborating other lines of evidence in formulating a more meaningful and useful classification of the family. More importantly it will help elucidate modes and mechanisms of speciation within the family.

MATERIALS AND METHODS

Cytological materials were obtained from the wild and fixed in Farmer's solution (3 anhydrous ethanol : 1 glacial acetic acid, v/v) or modified Carnoy's (Bradley 1948; Turner 1956) fluid (4 chloroform : 3 anhydrous ethanol : 1 glacial acetic acid, v/v/v). Fixed flower buds were immediately cooled on ice in the field and stored under refrigeration in the laboratory. All counts were made from acetocarmine squashes of pollen mother cells and observed with Zeiss phase contrast microscope. Chromosome drawings were made by camera lucida at magnifications of $\times 2600$ and $\times 2100$. Voucher specimens are deposited in the Jepson Herbarium, University of California at Berkeley, except where noted.

RESULTS AND DISCUSSION

In this study we present chromosome counts for 55 collections of 38 species representing eight genera (see Table 1). Included are what we believe to be the first counts for 17 species, indicated by an asterisk. In the following discussion, our counts are compared with the previously reported chromosome numbers for each genus. The

TABLE 1. GAMETIC CHROMOSOME NUMBERS OF WESTERN NORTH AMERICAN SCROPHULARIACEAE.

Taxon	Gametic chromosome number	Voucher
<i>Collinsia</i>		
<i>C. greenei</i> A. Gray	$n=7$	CALIFORNIA. Tehama Co.: Te-doc Mt., Heckard 2957.
* <i>C. linearis</i> A. Gray	$n=7$ (Fig. 1)	CALIFORNIA. Del Norte Co.: Middle Fork Smith River, below Patrick Creek, Heckard 6158.
* <i>Lamarouxia dasyantha</i> (Cham. & Schldl.) W. R. Ernst	$n=15$ (Fig. 2)	Mexico. OAXACA: 10 km N of Huajuapán de León, Breedlove 39190 (DS).
<i>Linaria</i>		
<i>L. dalmatica</i> (L.) Miller	$n=6$	ARIZONA. Coconino Co.: just E of Ashfork, Chuang & Chuang 7806.
<i>L. vulgaris</i> Miller	$n=6$	IDAHO. Blaine Co.: along US 95, 2 mi S of Custer Co. line, Heckard et al. 3471.
<i>Mimulus</i>		
* <i>M. arenarius</i> Grant	$n=16$ (Fig. 3)	CALIFORNIA. Fresno Co.: N Fork Kings River, Heckard & Chuang 3198.
* <i>M. bicolor</i> Hartweg ex Benth.	$n=8$ (Fig. 4)	CALIFORNIA. Mariposa Co.: Jersey Road, 8 mi NE of Mariposa, Heckard & Chuang 4062. Fresno Co.: 2 mi below Shaver Lake, Heckard & Chuang 5869.
* <i>M. bolanderi</i> A. Gray	$n=8$	CALIFORNIA. Fresno Co.: Jose Basin road, NE of Auberry, Walker 66012.
* <i>M. breweri</i> (E. Greene) Cov.	$n=16$ (Fig. 5)	CALIFORNIA. Colusa Co.: Snow Mt., Heckard & Hickman 5056.
* <i>M. filicaulis</i> S. Watson	$n=8$ (Fig. 6)	CALIFORNIA. Tuolumne Co.: S of Mather, Chuang & Chuang 7526.
<i>M. floribundus</i> Douglas ex Lindley	$n=16$	CALIFORNIA. Colusa Co.: Snow Mt., Heckard & Hickman 5729. Madera Co.: Ahwahnee, Heckard & Chuang 4067.
<i>M. guttatus</i> Fischer ex DC.	$n=14$	CALIFORNIA. Lassen Co.: S of Adin, Heckard & Chuang 5530. Lake Co.: W of Crockett Peak, Heckard & Hickman 5661.
* <i>M. layneae</i> (E. Greene) Jepson	$n=8$ (Fig. 7)	CALIFORNIA. Fresno Co.: Dinkey Creek road to McKinley Grove, Heckard & Chuang 3193.

TABLE 1. CONTINUED.

Taxon	Gametic chromosome number	Voucher
* <i>M. latidens</i> (A. Gray) E. Greene	$n=16$ (Fig. 8)	CALIFORNIA. Stanislaus Co.: SE of Warnerville, Heckard & Chuang 4746.
<i>M. moschatus</i> Douglas ex Lindley	$n=16$	CALIFORNIA. Tuolumne Co.: Stanislaus River, 3 mi NW of Columbia, Heckard & Chuang 5500.
<i>M. nanus</i> (E. Greene) Jepson	$n=8$	CALIFORNIA. Tehama Co.: Te-doc Mt., Heckard 2979.
* <i>M. pictus</i> (Curran) A. Gray	$n=8$ (Fig. 9)	CALIFORNIA. Kern Co.: Lilly Canyon, near Miracle Hot Springs, Bacigalupi & Hickman 9342.
* <i>M. pilosellus</i> E. Greene	$n=9$ (Fig. 10)	CALIFORNIA. Lake Co.: Snow Mt., Heckard & Hickman 5268. Mariposa Co.: Vogelsong Lake, Yosemite Natl. Park, Heckard 6781. Shasta Co.: King Creek Meadow, Lassen Volcanic Natl. Park, Heckard & Chuang 5148a.
<i>M. primuloides</i> Benth.	$n=9$ (Fig. 11)	CALIFORNIA. Mono Co.: Crowley Lake, Heckard & Chuang 4927.
	$n=18$ (Fig. 12)	CALIFORNIA. Shasta Co.: King Creek Meadow, Lassen Volcanic Natl. Park, Heckard & Chuang 5148b. Mariposa Co.: Bridalveil Campground, Yosemite Natl. Park, Heckard 5872.
* <i>M. pygmaeus</i> Grant	$n=9$ or 10 (Fig. 13)	CALIFORNIA. Plumas Co.: Lake Almanor, Heckard 5203 (plants raised from seed collected by J. T. Howell), Heckard 5250.
* <i>M. torreyi</i> A. Gray	$n=10$ (Fig. 14)	CALIFORNIA. Lassen Co.: NE of Westwood, Heckard 5255.
* <i>M. tricolor</i> Lindley	$n=9$ (Fig. 15)	CALIFORNIA. Stanislaus Co.: SE of Warnerville, Heckard 4745.
<i>Parentucellia viscosa</i> (L.) Carnel.	$n=24$	CALIFORNIA. Sonoma Co.: Pitkin Marsh, Chuang & Heckard 6904.
<i>Pedicularis</i>		
* <i>P. attolens</i> A. Gray	$n=8$ (Fig. 16)	CALIFORNIA. Lassen Co.: NE of Westwood, Heckard & Chuang 5259.
<i>P. densiflora</i> Benth. ex Hook.	$n=8$	CALIFORNIA. Marin Co.: 1 mi SW of Fairfax, Chuang & Chuang 7489.

TABLE 1. CONTINUED.

Taxon	Gametic chromosome number	Voucher
* <i>P. semibarbata</i> A. Gray	<i>n</i> =8 (Fig. 17)	CALIFORNIA. San Bernardino Co.: Bluff Lake, Heckard & Chuang 4091.
<i>Penstemon</i>		
<i>P. deustus</i> Douglas ex Lindley	<i>n</i> =8	OREGON. Josephine Co.: Elijah Mt., Oregon Cave Natl. Monument, Chuang & Chuang 7776.
* <i>P. purpusii</i> Brandegee	<i>n</i> =8 (Fig. 18)	CALIFORNIA. Lake Co.: Snow Mt., Heckard & Hickman 5102.
<i>Veronica</i>		
<i>V. alpina</i> L.	<i>n</i> =9	CALIFORNIA. Alpine Co.: Woods Lake, Heckard & Chuang 3772, 3779; Ebbetts Pass, Sangre de Cristo Range, Heckard & Chuang 3562. NEVADA. Elko Co.: E Humboldt Mts., Angel Lake, Heckard & Chuang 4957.
<i>V. americana</i> (Raf.) Benth.	<i>n</i> =18	CALIFORNIA. Mono Co.: 3 mi SE of Bridgeport, Heckard 2714a; 2 mi W of Bridgeport, Heckard 2817, 2818. Sonoma Co.: Pitkin Marsh, Chuang et al. 6905.
<i>V. anagallis-aquatica</i> L.	<i>n</i> =18	CALIFORNIA. San Joaquin Co.: 7 mi SW of Manteca, Heckard 2803. Siskiyou Co.: Shasta River, 5 mi N of Yreka, Heckard 2781.
<i>V. catenata</i> Pennell	<i>n</i> =18	CALIFORNIA. Siskiyou Co.: Shasta River, 5 mi N of Yreka, Heckard 2782. OREGON. Klamath Co.: 2 mi NE of Keno, Heckard 2698.
<i>V. copelandii</i> Eastw.	<i>n</i> =9	CALIFORNIA. Trinity Co.: Mt. Eddy, Middle Deadfall Lake, Heckard 2690.
<i>V. cusickii</i> A. Gray	<i>n</i> =9	CALIFORNIA. Alpine Co.: Wood Lake, Heckard 3778, 6774.
<i>V. peregrina</i> L. subsp. <i>xalapensis</i> (Kunth) Pennell	<i>n</i> =27	OREGON. Marion Co.: 1 mi NW of Aumsville, Heckard 2915.
<i>V. persica</i> Poiret	<i>n</i> =14	CALIFORNIA. Alameda Co.: Berkeley, Heckard 4068.
<i>V. scutellata</i> L.	<i>n</i> =9	CALIFORNIA. Sonoma Co.: Pitkin Marsh, Chuang et al. 6906. OREGON. Marion Co.: 1 mi NW of Aumsville, Heckard 2926.

TABLE I. CONTINUED.

Taxon	Gametic chromosome number	Voucher
<i>V. serpyllifolia</i> L. var. <i>humifusa</i> (Dickson) Vahl	$n=7$	CALIFORNIA. Colusa Co.: Snow Mt., Heckard & Hickman 5276. Modoc Co.: Cedar Pass, Warner Mts., Heckard 5241.

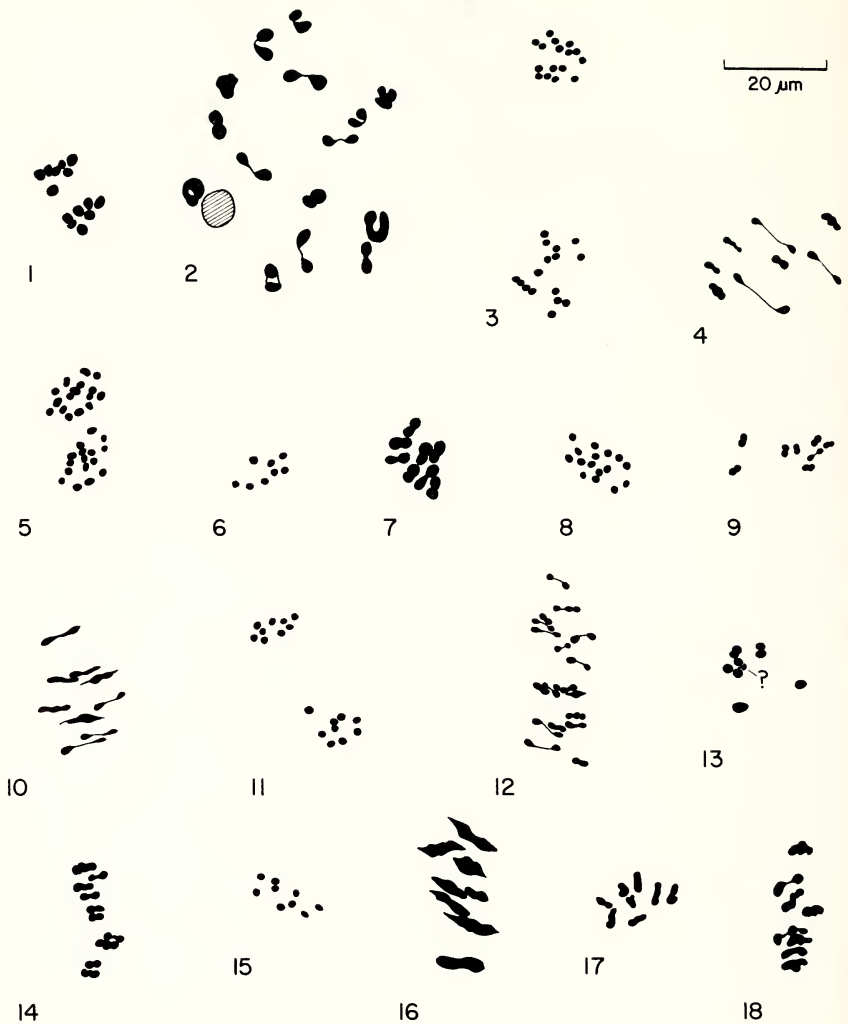
systematic implications based on chromosome number are briefly discussed where appropriate.

Collinsia Nutt. This genus, comprising 21 annual species, is restricted to western North America. All reported species are $n=7$, except *C. torreyi*, which is polyploid with $n=21$ (Garber 1956, 1958). Our count of $n=7$ for *C. greenii* agrees with the previously reported count by Garber (1958). The count of $n=7$ for *C. linearis* (Fig. 1) is the first for this species and confirms the base chromosome number of $x=7$ for the genus. Although Moldenke (1973) listed $2n=42$ for *C. linearis*, we are unable to find it in Garber's (1958) original report.

Lamourouxia Kunth. This genus, distributed from Mexico south to Peru, includes 24 perennial species (Ernst 1972). The three species reported thus far each has a different chromosome number: *Lamourouxia longiflora* (section *Lamourouxia*), $n=7$ (Ernst 1972); *L. viscosa* (section *Hemispadon*), $n=14$ (Ernst 1972); and *L. multifida* (section *Lamourouxia*), $n=16$ (Cruden 1972). Our count of $n=15$ for *L. dasyantha* (section *Adelphidion*; Fig. 2) is the first for this species and section. It appears that higher numbers of $n=14-16$ are polyploid, perhaps derived from amphiploid of ancestral forms with a base number of $x=7$, followed by aneuploid increase. More chromosome counts are needed for the genus, especially from Mexico, before any attempt to explore the utility of chromosome number in relation to the infrageneric classification can be realized.

Linaria Miller. This genus, composed of more than 100 species, is mostly Eurasian; only one species is native to North America. Two base chromosome numbers of $n=6$ and 7 have been reported for the genus, the former representing the prevalent number. Several polyploids based on $n=6$ have been reported (see Sutton 1980 for summary). Our counts of $n=6$ for both *L. dalmatica* and *L. vulgaris* agree with previous reports (Valdes 1970).

Mimulus L. This large genus of approximately 150 species of annual and perennial herbs and shrubs (section *Diplacus*) is distributed principally in western North America, especially California. Munz (1959) listed 77 species in that state and undoubtedly the California floristic province is a center of diversity of the genus.



FIGS. 1-18. Meiotic chromosome figures of first counts of western North American and Mexican Scrophulariaceae (H = Heckard; C = Chuang). 1. *Collinsia linearis*, $n=7$, TI (H-6158). 2. *Lamarouxia dasyantha*, $n=15$, Diak. (Breedlove 39190). 3. *Mimulus arenarius*, $n=16$, TI (H&C-3198). 4. *M. bicolor*, $n=8$, MI (H&C-4062). 5. *M. breweri*, $n=16$, $\frac{1}{2}$ portion of TII (H & Hickman 5056). 6. *M. filicaulis*, $n=8$, $\frac{1}{4}$ portion of TII (C&C-7526). 7. *M. layneae*, $n=8$, MI (H&C-3193). 8. *M. latidens*, $n=16$, $\frac{1}{4}$ portion of TII (H&C-4746). 9. *M. pictus*, $n=8$, MI (Bacigalupi & Hickman 9342). 10. *M. pilosellus*, $n=9$, MI (H&C-5148a). 11. *M. primuloides*, $n=9$, TI (H&C-4927). 12. *M. primuloides*, $n=18$, MI (H&C-5148b). 13. *M. pygmaea*, $n=9$ or 10?, MI (H-5250). 14. *M. torreyi*, $n=10$, MI (H-5255). 15. *M. tricolor*, $n=9$, $\frac{1}{4}$ portion of TII (H-4745). 16. *Pedicularis attolens*, $n=8$, MI (H&C-5259). 17. *P. semibarbata*, $n=8$, $\frac{1}{4}$ portion of TII (H&C-4091). 18. *Penstemon purpusii*, $n=8$, MI (H & Hickman 5102).

Recently, two additional species, *M. norrisii* and *M. shevockii*, were described from California by Heckard and Shevock (1985) and Heckard and Bacigalupi (1986), respectively. A comprehensive survey of pollen morphology of the genus was conducted by Argue (1980). He reported 117 species and varieties, classified them into five major and eight more tentative, minor pollen types, and concluded that, "The pollen morphological data correlate well with geographical and macromorphological data and, where the latter are ambiguous, often provide important clues toward the resolution of conflicting interpretations of infrageneric classification and generic delimitation." Available cytological information (Vickery 1978) reveals great diversity of chromosome number in the genus, with gametic numbers of $n=7, 8, 10, 11, 12, 14, 15, 16, 17, 23, 24, 28, 30, 31, 31, 32,$ and 46 . He reports that sections *Erythranthe* and *Diplacus* have the same number throughout ($n=8$ and $n=10$, respectively) whereas section *Simiolus* has an extensive mixoploid series of $n=13, 14, 15, 16, 24, 28, 30, 31, 32,$ and 46 (Vickery 1978).

Included in the present study are counts of 16 species, 11 of which are reported here for the first time. Four species agree with and one differs from previously reported counts.

Five species (*M. dudleyi*, *M. floribundus*, *M. moschatus*, *M. norrisii*, and *M. shevockii*) of section *Paradanthus* have been previously reported from California; all have $n=16$. We report here $n=16$ also for *M. floribundus* and *M. moschatus*, in agreement with earlier reported counts. Our counts of $n=9$ and 18 for *M. primuloides* differ from that of McArthur and Vickery (1970) who reported $n=17$ for this species from plants collected 1.5 km above Bumpass Hell, Mt. Lassen, Shasta Co., California, very near the locality where we obtained our material. The counts of $n=8$ for *M. bicolor* (Fig. 4) and *M. filicaulis* (Fig. 6), $n=9$ for *M. pilosellus* (Fig. 10), and $n=16$ for *M. arenarius* (Fig. 3) and *M. latidens* (Fig. 8) represent the first reports for these species. *Mimulus pilosellus* E. Greene was reduced to varietal status under *M. primuloides* by Smiley (1921) and completely synonymized to that species by Grant (1924); subsequent workers have followed this treatment. *Mimulus pilosellus* (Heckard and Chuang 5148a) and *M. primuloides* (Heckard and Chuang 5148b) grow together in Lassen Volcanic National Park. They can be distinguished by the small and densely pilose leaves and small flowers of the former versus the larger and less densely pilose leaves and large flowers of the latter. The fact that these two taxa frequently grow together in many localities in the Sierra Nevada, and that *M. pilosellus* has a chromosome number of $n=9$ (Fig. 10) and *M. primuloides* $n=18$ (Fig. 12) leads us to reinstate the former as a distinct species.

Four species of section *Eunanus* have been reported previously: *M. brevipes*, *M. cusickii*, and *M. nanus* with $n=8$ and *M. bigelovii*

with $n=16$. Our count of $n=8$ for *M. nanus* confirms the previous count for this species. We report here first counts for the following: $n=8$ for *M. bolanderi* and *M. layneae* (Fig. 7) and $n=10$ for *M. torreyi* (Fig. 14). *Mimulus mohavensis*, treated in the monotypic section *Mimulastrum* by Gray (1884) and subsequently followed by Grant (1924), was submerged in section *Eunanus* by Pennell (1951). The chromosome number of $n=7$ (Carlquist 1953) and tricolpate pollen (Argue 1980) found in *M. mohavensis*, along with its distinct corolla morphology and styler pubescence, readily distinguish this species from members of section *Eunanus*, which have $n=8$ or 10, 5–7 stephanocolpate pollen, and different corolla morphology. Based on these facts, it seems desirable to retain the monotypic section *Mimulastrum* for *M. mohavensis*.

Mimulus breweri, included in section *Paradanthus* by Grant (1924), was assigned to a monotypic section *Monimanche* by Pennell (1947), who considered it to be intermediate between the subgenera *Synplacus* and *Schizoplacus* in having an unsplit capsule septum of the former and persistent corolla of the latter. We report here the first count for this species as $n=16$ (Fig. 5). This chromosome number and possession of tricolporate pollen grains further confirm the close affinity of this species with subgenus *Synplacus*, especially section *Paradanthus* as suggested earlier by both Grant (1924) and Argue (1980).

Mimulus pictus (Fig. 9) and *M. tricolor* (Fig. 15), both with $n=9$, represent not only first counts for these two species but also for section *Oenoe*. The gametic chromosome number of $n=9$ is a new base number of the genus. *Mimulus pygmaeus*, a much reduced species from NE California, was treated in a monotypic section, *Microphyton*, by Pennell (1947), who suggested that, "It is presumably derived from section *Eunanus* ancestry." We present here the first report for this species with $n=9$ or 10? (Fig. 13). The uncertainty owes to the fact that there were always 2 or 3 pairs of sticky chromosomes at metaphase I. This difficulty is compounded by the extremely small- and solitary-flowered plants, of which we were unable to collect sufficient bud material for a good count. Based on the probable chromosome number of $n=9$ and its 5–7 stephanocolpate pollen grains, we follow Grant (1924) in placing *M. pygmaeus* in section *Oenoe*, rather than section *Eunanus*, as suggested by Pennell (1947) and Argue (1980).

More chromosome counts, especially in sections *Eunanus* and *Oenoe*, are needed in order to clarify the sectional relationships of the genus and for placement of species of uncertain affinity.

Parentucellia Viv. This is a small genus of two species, native to the Mediterranean region. *Parentucellia viscosa* is an introduced weed in western North America and has been reported to be $n=24$ (Hamblen 1954, 1955). Our count of $n=24$ confirms this earlier

count. *Parentucellia latifolia* has also been reported as $n=24$ (Markova and Ivanova 1973).

Pedicularis L. This, the largest genus of Scrophulariaceae with about 500 species, occurs chiefly in northern temperate and boreal regions, especially in the Old World. Approximately 23 species are indigenous to western North America. The great majority of species thus far reported are diploid with $n=8$, plus a few tetraploid of $n=16$. Only one species, *P. verticillata*, has been reported several times by various investigators to be $n=6$ (see Carr 1971 for summary). We report here $n=8$ for *P. densiflora*, which is in agreement with previous counts by Carr (1972) and Spellenberg (1971). Our counts of $n=8$ for *P. attolens* (Fig. 16) and *P. semibarbatus* (Fig. 17) represent the first reports for these two species.

Penstemon Schmidel. This, the largest genus of North American Scrophulariaceae, is composed of over 250 species and is native to North America with the vast majority of species occurring in western United States. According to Freeman (1983), the chromosome numbers of 39.6% of the species of *Penstemon* have been reported, with $n=8$ representing the number most commonly encountered. He estimated that fewer than 20% of the species counted are polyploid, with $n=16, 24, 32,$ and 48 . We report here $n=8$ for both *P. deustus* and *P. purpusii* (Fig. 18), the former agreeing with the previously reported count (Keck 1945) and the latter representing the first count.

Veronica L. This genus is composed of over 200 species, distributed in the North Temperate Zone, especially in the Old World. Ownbey (1959) listed 14 species of *Veronica* occurring in the Pacific Northwest, five native and the remainder introduced from the Old World. The great amount of cytological information available to date reveals a diversity of chromosome number, with base numbers of $x=7, 8,$ and 9 and varying levels of polyploidy up to $n=32$ and 34 . Polyploidy is common in the genus, with many species consisting of 2 or 3 ploidy levels (see Index to Plant Chromosome Numbers 1966–1987). Obviously, polyploidy has played an important role in evolution in the genus. We report here $n=7$ for *V. serpyllifolia* var. *humifusa*; $n=14$ for *V. persica*; $n=9$ for *V. alpina*, *V. copelandii*, *V. cusickii*, and *V. scutellata*; $n=18$ for *V. americana*, *V. anagallis-aquatica*, and *V. catenata*; and $n=27$ for *V. peregrina* subsp. *xalapensis*. All counts agree with earlier reported counts.

ACKNOWLEDGMENTS

We thank Lincoln Constance for review of the manuscript, Fei-Mei Chuang for laboratory assistance, and Linda Ann Vorobik for illustration.

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(Received 7 June 1991; revision accepted 30 Oct 1991.)